HOW DO NONREPRODUCTIVE GROUPS AFFECT POPULATION GROWTH?

Fabio Augusto Milner

Department of Mathematics, Purdue University
150 North University Street, West Lafayette, IN 47907-2067

ABSTRACT. I describe several models of population dynamics, both unstructured and gender structured, that include groups of individuals who do not reproduce. I analyze the effect that the nonreproductive group may have on the dynamics of the whole population in terms of the vital rates and the proportion of nonreproductive individuals, and we provide specific examples for real populations.

1. **Introduction.** The basic dynamics of a population depends on the interplay between reproduction and mortality. Long-term trends of population growth or decline are usually affected not by *temporary* changes in reproduction or mortality but rather by long-term or *permanent* changes in these vital dynamics parameters. Examples of the latter are the extremely significant reduction in mortality during the twentieth century triggered by various medical discoveries, such as penicillin, and the reduction in the mean number of progeny per woman that accompanied social conquests by women. One factor whose long-term effect on population growth has not been examined is the segregation of portions of the reproductive population into nonreproductive classes, such as same-sex isolation groups—prisoners, members of religious orders, or lifelong homosexuals—or other nonreproductive classes who by choice or for medical reasons remain childless for life. Under normal circumstances, childless individuals who are incarcerated for the entirety of their reproductive years will have no sexual contact with the opposite gender and therefore remain childless for life. Similarly, men and women who participate exclusively in homosexual relationships (or in none at all) for their entire lives will remain childless. Some of these groups (religious or incarcerated individuals isolated during all of their reproductive years) are quite small; others (lifelong homosexuals and individuals who choose or are forced by medical reasons not to have progeny) are not, and they may have a long-term effect on population growth. Thus, we see the importance of studying population models that take into consideration nonreproductive groups.

It is intuitively obvious that in a population closed to migration, if the segregation rate into nonreproductive groups is large enough, the population will decline and eventually extinguish itself. In contrast, in a population with a steady immigration of reproductive individuals, this is not the case: even if every individual in the population were segregated into nonreproductive groups, the external supply of new individuals would sustain a population, albeit an entire nonreproductive one.

Similar results can be expected for the fate of an infectious disease invading a population in which some proportion of infected individuals is isolated from all (infectious) contact with others for the duration of the infectious period. Sexually transmitted diseases, for example, represent such a situation when one considers not the reproduction of individuals per se but rather the reproduction of the disease, that is, its transmission from infected to susceptible. A significant number of individuals infected with herpes simplex type B, for example, refrain from sexual activity during outbreaks, when they are contagious. If a large enough proportion of them did this, the disease would eventually disappear. This situation and others, such as the efficacy of quarantine of infected individuals with SARS, will be analyzed in a forthcoming paper.

2. **One-sex, constant-fertility and mortality models.** The simplest unstructured demographic models prescribe a constant mortality rate per individual per unit of time, μ, and either a constant *total* birth rate per unit of time, Λ, or a constant per capita birth rate per unit of time, β.

The corresponding ordinary differential eqution (ODE) models are, respectively,

$$P'(t) = \Lambda - \mu P(t) \quad \text{and} \quad P'(t) = \beta P(t) - \mu P(t), \tag{1}$$

with solutions

$$P(t) = P(0)\, e^{-\mu t} + \frac{\Lambda}{\mu} \left(1 - e^{-\mu t}\right) \quad \text{and} \quad P(t) = P(0)\, e^{(\beta - \mu)t}. \tag{2}$$

Both models have monotone behavior for $P(0) > 0$—the former asymptotically converging to $\frac{\Lambda}{\mu}$, the latter growing (or decreasing) exponentially at Malthusian rate $r = \beta - \mu$.

These are usually too simplistic for long-term demographic projections, since many factors that influence the evolution of the size of human populations are not taken into account.

If we assume there is a uniform probability per unit of time, $\nu \geq 0$, that a randomly selected individual will not reproduce because of any of the reasons mentioned in the introduction (or for any other reason), then we can modify the unstructured models (1) as follows to reflect this particular behavior: let $R(t)$ and $N(t)$ denote the size of the reproductive and nonreproductive populations, respectively. Then, the dynamics of the reproductive group is described by one of the following equations,

$$R'(t) = \Lambda - \mu R(t) - \nu R(t) \quad \text{and} \quad R'(t) = \beta R(t) - \mu R(t) - \nu R(t), \tag{3}$$

while that of the nonreproductive group is described by

$$N'(t) = -\mu N(t) + \nu R(t). \tag{4}$$

The respective solutions for the reproductive group are

$$R(t) = R(0)\, e^{-(\mu+\nu)t} + \frac{\Lambda}{\mu+\nu} \left(1 - e^{-(\mu+\nu)t}\right) \text{ and } R(t) = R(0)\, e^{(\beta-\mu-\nu)t}, \tag{5}$$

while those for the nonreproductive one are

$$N(t) = \frac{\Lambda\nu}{\mu(\mu+\nu)} + \left[P(0) - \frac{\Lambda}{\mu}\right] e^{-\mu t} + \left[\frac{\Lambda}{\mu+\nu} - R(0)\right] e^{-(\mu+\nu)t}, \tag{6}$$

$$\begin{cases} N(t) = \left[N(0) - \dfrac{\nu R(0)}{\beta - \nu} \right] e^{-\mu t} + \dfrac{\nu R(0)}{\beta - \nu} e^{(\beta - \mu - \nu)t} \quad \text{(if } \beta \neq \nu), \\[3mm] N(t) = [N(0) + R(0)\nu t] \, e^{-\mu t} \quad \text{(if } \beta = \nu). \end{cases} \quad (7)$$

Of course, $\nu = N(0) = 0$ in (3)–(7) imply $R(t) \equiv P(t)$ and $N(t) \equiv 0$; whence (3) is the same as (1) and (5) is the same as (2).

Next, note that by summing (5) with (6) and (7), we obtain explicit formulas for the total population size, $P = R + N$, for each model:

$$P(t) = \frac{\Lambda}{\mu} + \left[P(0) - \frac{\Lambda}{\mu} \right] e^{-\mu t}, \quad (8)$$

$$\begin{cases} P(t) = \left[N(0) - \dfrac{\nu R(0)}{\beta - \nu} \right] e^{-\mu t} + \dfrac{\beta R(0)}{\beta - \nu} e^{(\beta - \mu - \nu)t} \text{ (if } \beta \neq \nu), \\[3mm] P(t) = [P(0) + R(0)\nu t] \, e^{-\mu t} \text{ (if } \beta = \nu). \end{cases} \quad (9)$$

Comparing (2) and (8), we can readily see that in the first model the effect of the nonreproductive group on total population growth is nil. Also, from (6) and (8), we see that the proportion of nonreproductive individuals asymptotically approaches the value $\nu/(\mu + \nu)$.

On the other hand, concerning the second unstructured model in (1), we see from (9) that when $\beta > \mu$ and $\nu \neq \beta$, there is a threshold value for ν, $\nu_0 = \beta - \mu$, that leads to ultimate population extinction if it is surpassed. Moreover, combining (7) and (9), we see that the proportion of nonreproductive individuals in the total population asymptotically approaches 1 if $\beta \leq \nu$, and it approaches the ratio ν/β if $\beta > \nu$. The latter is possible for exponentially decreasing populations ($\beta < \mu + \nu$), bounded populations ($\beta = \mu + \nu$), or exponentially increasing ones ($\beta > \mu + \nu$).

We also note that in the case $0 \leq \beta - \mu = \nu_0 < \nu < \beta$, if $N0) = 0$, we can write

$$\begin{cases} P(t) = R(0) \left[\dfrac{\beta}{\beta - \nu} e^{(\beta - \mu - \nu)t} - \dfrac{\nu}{\beta - \nu} e^{-\mu t} \right], \\[3mm] P'(t) = R(0) \left[\dfrac{\beta(\beta - \mu - \nu)}{\beta - \nu} e^{(\beta - \mu - \nu)t} + \dfrac{\mu \nu}{\beta - \nu} e^{-\mu t} \right]. \end{cases} \quad (10)$$

Thus, we see that the population increases for $t \leq \frac{\ln\left(\frac{\mu \nu}{\beta(\mu + \nu - \beta)} \right)}{\beta - \nu}$, and then it decreases exponentially to 0. Similarly, for $\beta = \nu > \mu$, P increases for $t \leq \frac{\nu - \mu}{\mu \nu}$, and then it decreases exponentially to 0. If $\nu > \beta$, then P decreases exponentially to 0.

Example 1. I draw examples from Japan and Argentina based on real-life data. Note that the vital rates for Japan in 2001 were $\beta = 0.0093$ and $\mu = 0.0077$ [4], which result in a threshold value $\nu_0 = 0.0016$ for this last model. If there were no migration, a segregation rate from the reproductive population into the nonreproductive one exceeding just 0.16% per year would lead to population extinction. In the city of Buenos Aires, Argentina, for that same year the values were $\beta = 0.0139$ and $\mu = 0.0111$ [1], which result in a threshold value $\nu_0 = 0.0028$ for this last model. I show this last case in Figure 1. This threshold should be interpreted with caution as these values were estimated for the whole population, without consideration of its age distribution.

□

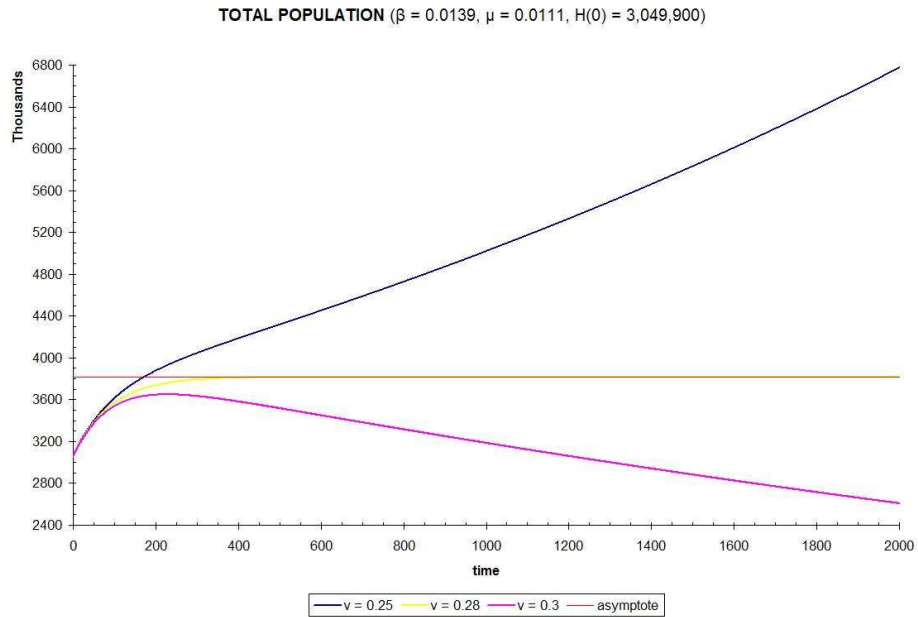**TOTAL POPULATION** (β = 0.0139, μ = 0.0111, H(0) = 3,049,900)

FIGURE 1. Example from Buenos Aires, Argentina, 2001.

3. **One-sex logistic models.** A better model for long-term projections than either model (1) is that of logistic growth:

$$P' = r \left(1 - \frac{P}{K}\right) P, \tag{11}$$

where K is the carrying capacity of the environment and r is the Malthusiam rate, with solution

$$P(t) = \frac{K}{1 + \left[\frac{K}{P(0)} - 1\right] e^{-rt}},$$

asymptotically approaching the value K for any nonzero initial value $P(0)$.

We can also modify the logistic model (11) to include segregation into a nonreproductive class as follows:

$$\begin{cases} R' &= (\beta - \mu) \left(1 - \frac{P}{K}\right) R - \nu R, \\[2mm] N' &= -\mu N - (\beta - \mu)\frac{P}{K} N + \nu R, \end{cases} \tag{12}$$

where the total population is then modeled by

$$P' = (\beta - \mu) \left(1 - \frac{P}{K}\right) P - \nu N.$$

Unfortunately, there is no explicit form of the solution of (12) for $\nu > 0$. However, the first equation in (12) exhibits a threshold phenomenon that separates population persistence from population extinction. Clearly, if $\nu > \beta - \mu > 0$, then $R(0) e^{-(\mu+\nu-\beta)t}$ is a supersolution, and thus R must asymptotically approach zero.

On the other hand, if $\nu < \beta - \mu$, then $R' = (\beta - \mu - \nu)\,R - (\beta - \mu)\frac{P}{K}\,R$ is positive as soon as $P < K\,(1 - \frac{\nu}{\beta - \mu})$, giving a positive lower limit for P. In this sense, we see that the logistic model exhibits the same threshold behavior as Malthus's exponential growth model: when $\beta > \mu$, they both represent declining populations that go asymptotically extinct if $\nu > \beta - \mu$, and they both have populations that persist for all time if $\nu < \beta - \mu$—the former asymptotically approaching a finite positive limit, the latter growing exponentially at rate $r = \beta - \mu - \nu$.

Figure 2 presents the reproductive and the total population sizes obtained from numerical solutions of (12) using the initial size, mortality and fertility rates from the actual U.S. population in 2000: $R(0) = P(0) = 281$ million, $N(0) = 0$, carrying capacity $K = 300$ million (chosen just for reference), mortality rate $\mu = 0.01303$, per capita birth rate $\beta = 0.01442$, and several values of the segregation rate ν. I show the behavior of the logistic model in the absence of the nonreproductive group ($\nu = 0$), as well as the reproductive group size and the total population size when the segregation rate is $\nu = 0.000125$, 0.00025, 0.0005, 0.001, and 0.002. The proportion of heterosexual individuals in the total population asymptotically stabilizes to lower values with increasing ν at approximately 99% for $\nu = 0.000125$, 98% for $\nu = 0.00025$, 97% for $\nu = 0.0005$, and 93% for $\nu = 0.001$. Of course, for $\nu = 0.002 > \beta - \mu$, the entire population asymptotically declines to extinction.
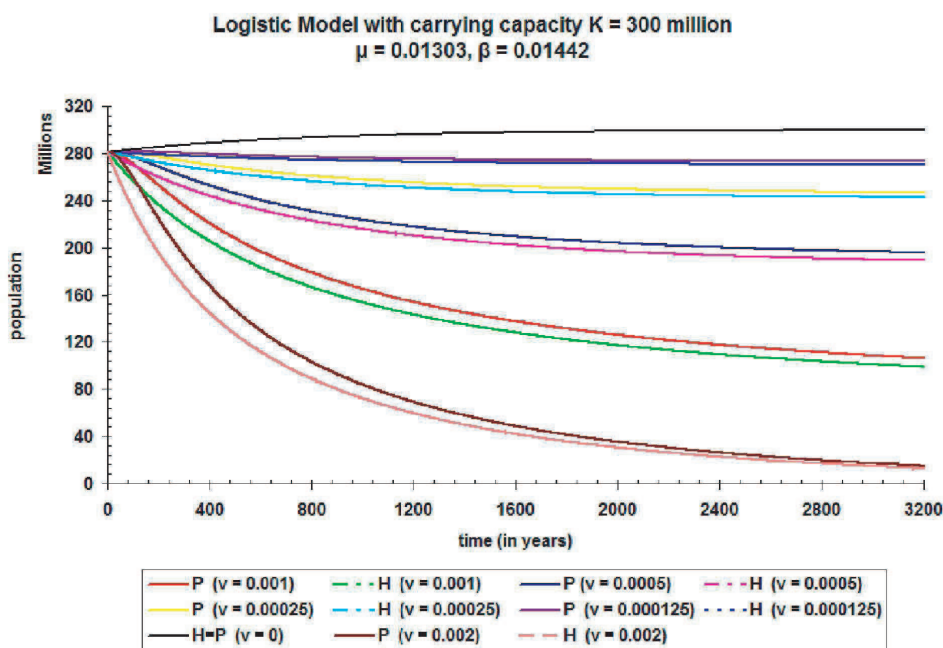

FIGURE 2. Example of the effect of segregation in logistic growth.

4. **Two-sex models.** When trying to model sexual reproduction, a simple model due to Kendall [2] is described in terms of the numbers of uncoupled females, F, uncoupled males, M, and reproductive couples, C. Now, let μ_f and μ_m be the

per capita mortality rates of females and males respectively, β represent the per-couple birth rate per unit of time, γ represent the proportion of newborn males among all newborn (e.g., $\gamma = \frac{2,076,969}{4,058,815} = 0.511718$ for the United States in 2000), δ be the per-couple divorce rate per unit of time, and $\mathcal{M}$ represent the coupling function giving the number of new reproductive pairings per unit of time when F single (i.e., uncoupled) female and M single male individuals are present in the population. Then, the ODE model is given by

$$\begin{cases} F' & = -\mu_f\, F + (1-\gamma)\beta\, C - \mathcal{M}(F,M) + \delta\, C, \\[2mm] M' & = -\mu_m\, M + \gamma\beta\, C - \mathcal{M}(F,M) + \delta\, C, \\[2mm] C' & = -(\delta + \mu_f + \mu_m)\, C + \mathcal{M}(F,M). \end{cases} \tag{13}$$

Now let ν_f and ν_m be the probability per unit of time that a single (uncoupled) female or male newborn, respectively, will never reproduce (for any reason). Then, modify (13) as follows:

$$\begin{cases} F' & = -\mu_f\, F - \nu_f\, F + (1-\gamma)\beta\, C - \mathcal{M}(F,M) + \delta\, C, \\[2mm] M' & = -\mu_m\, M - \nu_m\, M + \gamma\beta\, C - \mathcal{M}(F,M) + \delta\, C, \\[2mm] C' & = -(\delta + \mu_f + \mu_m)\, C + \mathcal{M}(F,M). \end{cases} \tag{14}$$

If we let $\varphi(t)$ and $\chi(t)$ represent the numbers of nonreproductive females and males, respectively, in the population at time t, then we can model their dynamics as follows:

$$\begin{cases} \varphi' = -\mu_f\varphi + \nu_f\, F, \\[2mm] \chi' = -\mu_m\chi + \nu_m\, M. \end{cases} \tag{15}$$

There is no explicit solution to the system (14)–(15) in general. However, if we make the assumptions $\gamma = \frac{1}{2}$, $\mu_f = \mu_m$, $\nu_f = \nu_m$, $\mathcal{M} = 2\rho\frac{FM}{F+M}$, and $F(0) = M(0)$, it follows that $F(t) = M(t)$ for all $t \geq 0$ and system (14) reduces to

$$\begin{cases} F' & = -(\mu + \nu)\, F + \frac{\beta}{2}\, C - \rho\, F + \delta\, C, \\[2mm] C' & = -(\delta + 2\mu)\, C + \rho\, F, \end{cases} \tag{16}$$

while assuming in addition that $\varphi(0) = \chi(0)$ implies $\varphi(t) \equiv \chi(t)$. It is possible to determine conditions on the demographic rates that will make F a multiple of C and further reduce system (16) to a single ODE that can be explicitly solved. Letting $F = \alpha C$ in (16), we see that

$$\alpha\, C' = -(\mu + \nu)\alpha\, C + \frac{\beta}{2}\, C - \rho\alpha\, C + \delta\, C = -(\delta + 2\mu)\alpha\, C + \rho\alpha^2\, C,$$

whereby

$$\rho\,\alpha^2 + (\rho + \nu - \mu - \delta)\,\alpha - \left(\frac{\beta}{2} + \delta\right) = 0. \tag{17}$$

Since the discriminant of this equation is always positive, it follows that the equation has two real roots, one positive and one negative. The positive one,

$$\alpha = \frac{\mu + \delta - \rho - \nu + \sqrt{(\rho + \nu - \mu - \delta)^2 + 2\rho\,(\beta + 2\delta)}}{2\rho}, \tag{18}$$

gives again the multiplier that relates F and C. With this value of α, we now solve the second equation in (16) for C (namely, $C' = r_\nu C$):

$$C(t) = C(0)\, e^{r_\nu t},$$

with Malthusian rate $r_\nu = \rho\alpha - \delta - 2\mu$, dependent on ν through α. Finally, we obtain for the singles

$$F(t) = M(t) = \alpha\, C(0)\, e^{r_\nu t} = F(0)\, e^{r_\nu t},$$

and, solving (15) using this expression for F, we obtain for the nonreproductive group

$$\begin{cases} \varphi(t) = \left[\varphi(0) - \dfrac{\alpha\nu C(0)}{\mu + r_\nu}\right] e^{-\mu t} + \dfrac{\alpha\nu C(0)}{\mu + r_\nu}\, e^{r_\nu t} & \text{(if } \rho\alpha \neq \mu + \delta), \\[3mm] \varphi(t) = [\varphi(0) + \alpha\nu C(0)\, t]\, e^{-\mu t} & \text{(if } \rho\alpha = \mu + \delta). \end{cases} \tag{19}$$

The total population size, $P(t) = 2\big[F(t) + \varphi(t) + C(t)\big]$, is now

$$\begin{cases} P(t) = 2\left[1 + \alpha + \dfrac{\alpha\nu}{\mu + r_\nu}\right] C(0)\, e^{r_\nu t} + 2\left[\varphi(0) - \dfrac{\nu F(0)}{\mu + r_\nu}\right] e^{-\mu t} & \text{(if } \rho\alpha \neq \mu + \delta), \\[3mm] P(t) = 2\left[1 + \alpha\right] C(0)\, e^{r_\nu t} + 2\left[\varphi(0) + \alpha\nu C(0)\, t\right] e^{-\mu t} & \text{(if } \rho\alpha = \mu + \delta). \end{cases} \tag{20}$$

It follows from (19) and (20) that the proportion of nonreproductive individuals in the population asymptotically approaches 1 if $\rho\alpha \leq \mu + \delta$, and it approaches the ratio $\alpha\nu/[\alpha\nu + (\alpha + 1)(\rho\alpha - \delta - \mu)]$ if $\rho\alpha > \mu + \delta$.

Notice from (18) that

$$r_\nu = \rho\alpha - \delta - 2\mu = \frac{-(3\mu + \rho + \nu + \delta) + \sqrt{(\rho + \nu - \mu - \delta)^2 + 2\rho\,(\beta + 2\delta)}}{2}$$

vanishes if, and only if, $(\rho + \nu - \mu - \delta)^2 + 2\rho\,(\beta + 2\delta) = (3\mu + \rho + \nu + \delta)^2$ or, equivalently,

$$\nu = \frac{\rho\beta - 2\mu(2\mu + 2\rho + \delta)}{2(\delta + 2\mu)}. \tag{21}$$

If we assume that in the absence of nonreproductive groups the population increases exponentially at the rate

$$r_0 = \frac{-(3\mu + \rho + \delta) + \sqrt{(\rho - \mu - \delta)^2 + 2\rho\,(\beta + 2\delta)}}{2} > 0,$$

it follows that $(\rho - \mu - \delta)^2 + 2\rho\,(\beta + 2\delta) > (3\mu + \rho + \delta)^2$; that is,

$$\rho\beta - 2\mu(2\mu + 2\rho + \delta) > 0.$$

Thus, we see from (21) a threshold effect, whereby a rate of passage into nonreproductive groups

$$\nu_f = \nu_m = \nu = \frac{\rho\beta - 2\mu(2\mu + 2\rho + \delta)}{2(\delta + 2\mu)} > 0$$

would stop the exponential growth and result in a stagnant population. Higher values of ν would asymptotically lead to population extinction.

Next, let us assume $M(t) = F(t)$ for all time and the harmonic mean marriage function, and let us look for exponential solutions with $M = F = \alpha C$. We see from (14) that

$$-\alpha(\mu_f + \nu_f) + \beta(1 - \gamma) = -\alpha(\mu_m + \nu_m) + \beta\gamma. \tag{22}$$

It follows from (22) that either

$$\mu_m + \nu_m = \mu_f + \nu_f \quad \text{and, necessarily,} \quad \gamma = \frac{1}{2}$$

or

$$\mu_m + \nu_m \neq \mu_f + \nu_f \quad \text{and, necessarily,} \quad \alpha = \frac{\beta(2\gamma - 1)}{(\mu_m - \mu_f) + (\nu_m - \nu_f)}. \qquad (23)$$

The first case leads, of course, to (16). In the second case, however, α also needs to satisfy the relation $\rho\alpha^2 + (\rho - \mu_f + \nu_m - \delta)\alpha - (\beta\gamma + \delta) = 0$, corresponding to (17) for this case, giving the following necessary condition for $F(t)$ to be identical to $M(t)$ for all time in the case of unequal vital rates for the two genders:

$$\frac{\mu_f + \delta - \rho - \nu_m + \sqrt{(\rho - \mu_f + \nu_m - \delta)^2 + 4\rho(\beta\gamma + \delta)}}{2\rho} = \frac{\beta(2\gamma - 1)}{(\mu_m - \mu_f) + (\nu_m - \nu_f)}. \tag{24}$$

Of course, $\nu_f = \nu_m = 0$ together with $\phi(0) = \chi(0) = 0$ reduce (14) to (13), thus simplifying case (18) to

$$\alpha = \frac{\mu + \delta - \rho + \sqrt{(\rho - \mu - \delta)^2 + 2\rho(\beta + 2\delta)}}{2\rho}, \qquad (25)$$

giving the multiplier that relates F and C.

The total population in this case is given by $P = 2F + 2C = 2(\alpha + 1)C$; that is, $C = \frac{1}{2(\alpha+1)}P$. Therefore, using (16), we see that it satisfies $P' = rP$, with

$$r = \frac{\beta - 2\mu(\alpha + 2)}{2(\alpha + 1)}. \qquad (26)$$

Notice from (25) and (26) that

$$r = \rho\alpha - \delta - 2\mu > 0$$

$$\iff (\rho - \mu - \delta)^2 + 2\rho(\beta + 2\delta) > (3\mu + \rho + \delta)^2$$

$$\iff 2\mu(2\mu + \delta) < \rho(\beta - 4\mu)$$

$$\iff \beta > 4\mu \quad \text{and} \quad \rho > 2\mu\frac{2\mu + \delta}{\beta - 4\mu}.$$

This says that the population will increase provided conditions $\beta > 4\mu$ and $\rho > 2\mu\frac{2\mu + \delta}{\beta - 4\mu}$ are both satisfied. The first condition means that the fertility rate must exceed the total mortality rate, while the second means that the marriage rate is sufficiently large to produce enough newborn.

It is easy to verify that $\lim_{\rho \to \infty} \alpha = 0$, as it should necessarily be so, since in the limiting case $\rho \to \infty$ all individuals are married, making $F = 0\,C$. Also, $\lim_{\rho \to \infty} r = \frac{1}{2}(\beta - 4\mu)$, which reconciles the two-sex model with the one-sex model, since (16) has, in this limiting case, a fertility rate $\beta/2$ (i.e., the average couple produces that many female newborns and an equal number of male newborns that instantaneously become $\beta/2$ new couples), while the mortality rate for couples is 2μ, independent of the value of δ, as divorce has no effect on the number of couples when the marriage rate is infinitely large.

We see from (23) that in the absence of nonreproductive groups, since α is greater than 0, $\gamma > \frac{1}{2}$ implies $\mu_m > \mu_f$. This is actually the case for human populations.

Example 2. As indicated earlier, for the United States in 2000, $\gamma = 0.5117$ and the mortality rates, computed as reciprocals of the life expectancy at birth, were $\mu_f = 0.01258$ and $\mu_m = 0.01350$ [3]. For that same year, $\beta = 0.07338$ (approximately 4.059 million births from 55.311 million couples), making $\alpha = 1.8664$. However, α also needs to satisfy the relation $\rho\alpha^2 + (\rho - \mu_f - \delta)\alpha - (\beta\gamma + \delta) = 0$, corresponding to (25) for this case, giving the following necessary condition for $F(t)$ to be identical to $M(t)$ for all time in the case of unequal vital rates for the two genders:

$$\alpha = \frac{\mu_f + \delta - \rho + \sqrt{(\rho - \mu_f - \delta)^2 + 4\rho\,(\beta\gamma + \delta)}}{2\rho} = \frac{\beta\,(1 - 2\gamma)}{\mu_f - \mu_m}. \qquad (27)$$

In the 2000 there were approximately 2,376,000 marriages among approximately 88.057 million unmarried females and 82.743 million unmarried males, resulting in $\rho = 0.027849$. It then follows from (27) that δ must satisfy the relation

$$\delta = \frac{\zeta^2 - 4\rho\beta\gamma - (\rho - \mu_f)^2}{2(\rho + \mu_f + \zeta)},$$

where

$$\zeta = \frac{2\rho\beta\,(1 - 2\gamma)}{\mu_f - \mu_m} + \rho - \mu_f.$$

Finally we see that with $\zeta = 0.1192$, $\delta = 0.03069$, and initial conditions

$$F(0) = M(0) = 1.8664\,C(0), \qquad (28)$$

the system (13) would have the solution $F(t) = M(t) = 1.8664\,C(0)\,e^{rt}$, with Malthusian growth rate $r = \rho\alpha - \delta - \mu_f - \mu_m = -0.004795$. This "model" population decreases at a rate of approximately 0.5% per year. Although the total numbers of unmarried females, unmarried males, and married couples in the United States in 2000 do not satisfy (28), note that the actual divorce rate for 2000 computed as the ratio of 0.9572 million divorces (excluding those from California, Indiana, Louisiana, and Oklahoma, where no divorce statistics are recorded) to an estimated 45.784 million married couples outside those four states—a number obtained as the proportion of the U.S. population living outside those four states multiplied by $C(0) = 55.311$ million couples in the U.S.—is $\delta = 0.02091$, approximately 33% lower than 0.03069. For this reason, it is to be expected that the Malthusian growth rate of the "model" population should be lower than that of the actual U.S. population found from the one-sex model (1), $r = \beta - \mu = 0.01442 - 0.01303 = 0.00139$, or approximately 0.14% per year.

These calculations underscore the importance of distinguishing among the two sexes when trying to determine the Malthusian rate for a human population, since the assumption that their numbers are identical may result in errors in the Malthusian rate that could make it uncertain whether the population is increasing or decreasing. Let us redo these calculations in Example 3 without assuming that the numbers of females and males are identical for all time.

It is worth noting that using $\delta = 0.02091$ in (27), we obtain $\alpha = 1.55365$, and then using the right-hand side of (27), we find $\mu_m = 0.013685$—just 1.4% larger than the actual per capita male mortality rate for the United States in 2000. This observation stresses the sensitivity of these calculations to changes in some of the parameters involved.

Finally, let us remark that using the actual vital rates the right-hand side of (27) gives $\alpha = 1.8664$, and thus $\delta = \alpha\rho - r - \mu_f - \mu_m = 1.8664\,\rho - 0.02747$. Substituting

this relation in the first equality of (27), we see that there is no solution for ρ—positive or negative. This summarizes the fact that the actual vital rates for the United States in 2000 do not correspond to those of a two-sex population with equal numbers of females and males for *any* marriage and divorce rates.

$\square$

In general, if we assume marriages take place according to the harmonic mean and still look for exponential solutions with a common Malthusian rate, we can set $F = \alpha C$, $M = \xi C$, and letting $\sigma = \delta + \mu_f + \mu_m$ be the separation rate per couple, we immediately obtain from (13)

$$\begin{cases} -\alpha \mu_f + \beta(1 - \gamma) - 2\rho \dfrac{\alpha \xi}{\alpha + \xi} + \delta = -\alpha \sigma + 2\rho \dfrac{\alpha^2 \xi}{\alpha + \xi}, \\[2mm] -\xi \mu_m + \beta \gamma - 2\rho \dfrac{\alpha \xi}{\alpha + \xi} + \delta \quad = -\xi \sigma + 2\rho \dfrac{\alpha \xi^2}{\alpha + \xi}, \end{cases} \tag{29}$$

and subtracting these relations side-by-side,

$$(\xi \mu_m - \alpha \mu_f) + \beta(1 - 2\gamma) = (\alpha - \xi) \left[2\rho \frac{\alpha \xi}{\alpha + \xi} - \sigma \right],$$

whereby if $\alpha \neq \xi$,

$$2\rho \frac{\alpha \xi}{\alpha + \xi} - \sigma = \frac{\beta(1 - 2\gamma) + (\xi \mu_m - \alpha \mu_f)}{\alpha - \xi}. \tag{30}$$

Combining (13) with (30), we see that $C(t) = C(0) e^{rt}$, where the Malthusian rate is

$$r = \frac{\beta(1 - 2\gamma) + (\xi \mu_m - \alpha \mu_f)}{\alpha - \xi}. \tag{31}$$

Next, multiplying both sides of the equations by $(\alpha + \xi)$, we rewrite system (29) in the following form:

$$\begin{cases} \xi \left[\beta(1 - \gamma) + \delta + (\sigma - \mu_f - 2\rho - 2\rho\alpha)\alpha \right] = \left[(\mu_f - \sigma)\alpha - \beta(1 - \gamma) - \delta \right]\alpha \\[2mm] \alpha \left[\beta \gamma + \delta + (\sigma - \mu_m - 2\rho - 2\rho\xi)\alpha \right] \quad = \left[(\mu_m - \sigma)\xi - \beta \gamma - \delta \right]\xi, \end{cases}$$

which can be readily rearranged as

$$\begin{cases} \xi = \dfrac{\left[(\mu_f - \sigma)\alpha - \beta(1 - \gamma) - \delta \right]\alpha}{\beta(1 - \gamma) + \delta + (\sigma - \mu_f - 2\rho - 2\rho\alpha)\alpha} \\[3mm] (-2\rho\alpha + \sigma - \mu_m)\xi^2 + \left[(\sigma - \mu_m - 2\rho)\alpha + \beta \gamma + \delta \right]\xi + (\beta \gamma + \delta)\alpha = 0. \end{cases} \tag{32}$$

If we now substitute the first equation in (32) into the second, we obtain a quintic for α, whose positive real roots (if any), together with (32.2), lead to the desired exponential solution.

Example 3. Using the data for the population of the United States in 2000 as given in Example 2, we have $\sigma = 0.04699$, $\xi = -\frac{-0.03441\alpha^2 - 0.05674\alpha}{-0.055698\alpha^2 - 0.021288\alpha + 0.05674}$, and

$$(-0.055698\alpha + 0.03349)\,\xi^2 + (-0.022208\alpha + 0.058458546)\,\xi + 0.058458546\alpha = 0,$$

that is,

$$\xi = \frac{(0.022208\alpha - 0.058459) \pm \sqrt{0.013517\alpha^2 - 0.010428\alpha + 0.0034174}}{0.06698 - 0.11140\alpha}.$$

There is a unique real positive solution, $(\alpha, \xi) = (1.536, 1.568)$. Using (31), it gives a growth rate $r = -0.00400$. Note that the Malthusian rate computed in Example 2, assuming equal numbers of females and males, is 20% smaller than the value we just found, stressing again the quantitative importance of keeping the sexes separate in the model.

$\square$

As a final remark, I shall explain why the Malthusian rate computed from the two-sex model is so much smaller than that computed from the one-sex model—indeed, the former is negative while the latter is positive. In the one-sex model, the whole population is reproductive, and the only two parameters that may affect its long-term growth are the vital rates, that is, the fertility and mortality rates. In the two-sex model under consideration, only couples are reproductive, and therefore if a two-sex population is to grow, it is not only necessary that fertility exceed total mortality but also that there be enough marriages—as indicated in the argument following (26). The necessary and sufficient conditions derived for the case $\gamma = \frac{1}{2}$ and gender-independent vital rates are $\beta > 4\mu$ and $\rho > 2\mu \frac{2\mu+\delta}{\beta-4\mu}$. The analogous conditions when the vital rates differ among the sexes are $\beta > 2(\mu_f + \mu_m)$ and $\rho > \frac{\sigma(\mu_f + \mu_m)}{\beta - 2(\mu_f + \mu_m)}$. For the population of the United States in 2000, the first one is clearly satisfied and the second one is clearly not. This is the real reason why the Malthusian rate for the two-sex model population that results from using the actual data for 2000 is negative. Part of the problem can be solved by considering births not only from couples but from single females as well. Thus, a need for even more detailed models arises; some already exist, and others will be developed elsewhere.

5. **Conclusions.** I considered several simple population models and introduced in them nonreproductive classes that may represent, for example, lifelong childless homosexuals, individuals incarcerated until the end of their reproductive years, or others. I studied the effect that such groups can have on the growth of the total population.

For the simplest model, a "learning curve" corresponding to a population with a constant external supply of new individuals, I showed that the segregation into a nonreproductive group does not alter the growth dynamics of the total population, but rather it structures it into a reproductive class consisting of a proportion $\frac{\mu}{\mu+\nu}$ of the total and a nonreproductive class consisting of a proportion $\frac{\nu}{\mu+\nu}$ of the total.

For the next simplest model, Malthus's exponential model, I showed that the segregation into a nonreproductive group can indeed alter the population trend and make an exponentially increasing population stagnate or decline (depending on how the per capita birth rate compares with the sum of the mortality and segregation rates) and that the proportion of nonreproductive individuals in the total population will either approach 1 or the ratio $\frac{\nu}{\beta}$ (depending on whether $\beta \le \nu$ or $\beta > \nu$).

For the logistic model, I showed similar results; namely, the segregation into a nonreproductive group can indeed alter the population trend and make an increasing logistic population stagnate or decline (depending on how the per capita birth rate compares with the sum of the mortality and segregation rates). However, this time I could not derive this time an explicit expression for the asymptotic proportion of nonreproductive individuals in the population.

Some important behavioral considerations of human populations are neglected in the models in this paper, such as the role and of bisexual individuals in population

growth, births from homosexual females, return of individuals from homosexual groups to heterosexual ones, differences in contact rates among homosexuals forming couples and those who do not, and others. These issues will be addressed in a forthcoming paper.

Finally, the importance of segregation in population control discussed in this paper will be extended to the context of disease transmission and control for sexually transmitted diseases. The effect of isolating infectious individuals from sexual activity on the decline of disease prevalence will be analyzed elsewhere. There is an obvious analogy between the effect that the segregation of reproductive individuals into nonreproductive groups has on population growth and the effect that the segregation of individuals infected with a sexually transmitted disease into non-sexually-active groups will have on the growth of the infected class.

REFERENCES

[1] *Estadísticas Vitales—Información Básica Año 2001*, Ministerio de Salud, Dirección de Estadísticas e Información de la Salud, Deciembre 2002, Tabla 1, p. 6.

[2] D. G. Kendall, *Stochastic processes and population growth*, J. Roy. Stat. Soc. Ser. B 11 (1949), pp. 230–264.

[3] *Life Expectancy by Age, Race, and Sex*, National Vital Statistics Reports, December 2002, vol. 51, no. 3, Table 11, p. 29.

[4] *Population Statistics of Japan 2003*, National Institute of Population and Social Security Research, 2003, Table 3.1, p. 17.

E-mail address: milner@purdue.edu
URL: http://www.math.purdue.edu/~milner